菰属系统与演化研究──花粉形态*

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A SYSTEMATIC AND EVOLUTIONARY STUDY OF ZIZANIA L. (GRAMINEAE) — POLLEN MORPHOLOGY

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Abstract This paper deals with pollen morphology of Zizania L. and its relatives. A total of 7 genera, 13 species, 3 varieties and 1 form were examined under light microscope and scanning electron microscope. The results are as follows:

- 1. The genus Zizania belongs to tribe Oryzeae as shown by pollen characters, i. e. subspheroidal to ovoid in shape, monoporate, exine two-layered, with minute granules under LM.
- 2. The evolutionary trend of these taxa seems to be from minute granules free (Zizania latifolia, Z. texana, Zizaniopsis milicea and Oryza sativa) to minute granules aggregated in a group of 2—4 (many) (Zizania aquatica, Z. palustris, Leersia hexandra etc.). The genus Zizania may be derived from the ancient stock which has also given rise to the genus Oryza, and therefore parallel evolution may have taken place in Oryzeae, i. e. from perennial species to annual species in Zizania in one line, and from the genus Oryza to Leersia, Chikusichloa etc. in the other.
- 3. The characters of pollen morphology under LM and SEM support the division of the genus, Zizania into 4 species, 2 subspecies in the world, i. e. Z. latifolia (Griseb.) Turcz. ex Stapf, Z. texana Hitchc., Z. aquatica subsp. aquatica, Z. aquatica subsp. brevis (Fassett) S. L. Chen, Z. palustris subsp. palustris, and Z. palustris subsp. interior (Fassett) S. L. Chen.

Key words Zizania L.; Pollen morphology; Systematic evolution

摘要 本文首次报道了菰属 Zizania L. 及其有关属,共7属、13种、3变种、1变型的花粉形态。通过光学显微镜和扫描电镜,对其花粉的形状、外壁的层次及纹饰等进行了观察。经过研究,笔者认为: 菰属应置于禾本科稻族内;菰属在稻族内的演化及菰属内的种间演化均存在平行演化的现象; 菰属在全世界有4种2亚种。这些结论大都吻合笔者对其它形态特征的研究结果。

关键词 菰属;花粉形态;系统演化

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一、前言

菰属 Zizania L. 是禾本科 Gramineae 中一个既有经济价值又有学术意义的属。本属植物为优质饲料与饵料,其颖果 (Oelke, 1982) 营养价值的丰富为当前任何谷物所不及。它含 4 种,一种产东亚, 3 种产北美,是东亚与北美植物区系联系的纽带之一。全世界对其个别种或个别部分研究者众多,但对其系统位置及属、种处理等仍意见分歧(详见表 1 及表 2)。为了探讨菰属系统演化及处理其分类问题,应采用多学科途径。笔者自1985年开始,相继在叶片横切面、叶片表皮微形态、细胞等方面对其进行研究。本文为菰属及有关属(共 7 属13种 3 变种 1 变型)花粉形态研究结果的首次报道。

二、材料与方法

材料大都采自我们引种栽培的植株,少数取自江苏省植物研究所标本室、美国国家标本馆、美国密苏里植物园标本室及加拿大生物系统研究中心维管束植物标本室(详见表3)。

光学显微镜观察花粉制片用醋酸酐分解法处理 (Erdtman, 1969), 扫描电镜花粉均

表 1 各分类学者对蓝亚族、蓝族稻亚族等所含属数意见表

Table 1 Genera included in the subtribe Zizaniinae or tribe Zizanieae, Oryzeae etc. by various authors

人名 Author	观 点 Opinion	包含的属 Genera included
Honda (1930)	subtribe Zizaniinae	Zizania
	subtribe Chikusichlose	Chikusichloa
Hitchcock (1950)	tribe Zizanieae	Zizania, Zizaniopsis, Luziola,
		Hydrochlob, Pharus
Pilger (1954)	tribe Oryzeae	Oryza, Leersia, Hygroryza,
		Zizania, Zizaniopsis,
	_	Hydrochlos, Luziola,
		Chikusichloa
Keng (1959)	subtribe Zizaniinae	Zizania, Chikusichloa
Terrell et al. (1974)	subtribe Zizaniinze	Zizania
	subtribe Luziolinae	Zizaniopsis, Luziola
Tzvelev (1976)	subtribe Zizaniinae	Zizania, Zizaniopsis
Watson et al. (1985)	supertribe Oryzanae of subfam.	Brachyelytrum, Chikusichloa,
	Bambusoideae	Hydrochloa, Hygroryza,
		Lophatherum, Oryza,
		Phaenosperma, Pharus,
		Zizania, Zizaniopsis
Clayton et al. (1986)	tribe Oryzeae of subfam. Bambusoideae	Porteresia, Oryza, Leersia
		Rhynchoryza, Potamophila,
		Maltebrinia. Prosphytochloa,
	}	Chikusichloa, Hygroryza,
		Zizania, Zizaniopsis, Luziola
	tribe Phareac of subfam. Bambusoideae	Pharus, Leptaspis, Suddia

表 2 各分类学者对菰属下所含种类意见表

Table 2 Species recognized in Zizania L. by various authors

人 名 Author	包含的种类 species included	
Bentham (1991)	Z. aquatica L.	
Hitcncock (1950)	Z. aquatica L., Z. aquatica var. angustifolia Hitche., Z. texana	
	Hitche., Z. latifolia (Griseb.) Turcz. ex Stapf	
Tzvelev (1971)	Z. aquatica L., Z. aquatica subsp. angustifolia (Hitchc.) Tzvel.,	
	Z. texana Hitche., Z. latifolia (Griseb.) Turcz. ex Stapf	
Terrell, Warwick	Z. aquatica L. var. aquatica, Z. aquatica var. brevis Fassett, Z.	
et al.(1979—1986)	aquasica var. subbrevis Boivin, Z. palustris var. palustris, Z.	
61 an(17/7-1700)	palustris var. palustris f. purpurea Dore, Z. palustris var.	
	interior (Fassett) Dore, Z. texana Hitche. Z. latifolia (Griseb.)	
	Turcz, ex Stapf	
Chen (1989)	Z. aquatica L. subsp. aquatica, Z. aquatica L. subsp. brevis	
	(Fassett) S. L. Chen, Z. palustris subsp. palustris, Z. palustris	
	subsp. interior (Fassett) S. L. Chen, Z. texana Hitchc., Z.	
	latifolia (Griseb.) Turcz. ex Stapf	

为未经分解处理的花粉,用金箔喷镀后在 S-10型扫描电镜下观察。

三、结果与讨论

本实验研究结果,对菰属的系统位置及演化途径与分类上的一些处理,大都类似其它形态特征的研究结果(陈守良等 1982,1989; 黄真生 1978; Clayton 和 Renvoize 1986; Erdtman 1969; Hirayoshi 1957; Hoshikana 1969; Metcalfe 1960; Terrell 和 Wergin 1979, 1981),可归纳如下:

- (一) 花粉形态: 在光学显微镜下观察,花粉近球形或卵球形;远极单孔; 外壁 2 层, 纹饰为细颗粒状。其详细特征详见表 4 与图版 1—2。
- (二) 系统位置: 菰属的花粉形态,在光学显微镜下为近球形或卵球形,远极单孔等类似稻族中的稻属 Oryza、假稻属 Leersia 等;在扫描电镜下的菰 Zizania latifolia, 得克萨斯菰 Zizania texana, 水稻 Oryza sativa 及拟菰 Zizaniopsis miliacea 等的花粉外壁纹饰均为分离的细小颗粒;而两种一年生菰 (Z. aquatica, Z. palustris) 与秕谷草 Leersia sayanuka Ohwi 等的花粉外壁大都为 2-4 细颗粒聚成团。 以上均说明菰属应位于禾本科的稻族 tribe Oryzeae 中。
- (三)演化关系:在花粉外壁纹饰上,两种多年生菰所具分离的细小颗粒近似水稻及拟菰;两种一年生菰所具 2—4 细颗粒聚成团的外壁纹饰类似秕谷草 Leersia sayanuka Ohwi。根据生长习性的演化规律,两种多年生菰比两种一年生菰原始;又根据禾本科中小穗的演化规律为假稻属 Leersia Swartz 的小穗退化仅剩一小花的现象比稻属进化的情况,可推测禾本科的孢粉外壁纹饰在稻族中的系统演化上,应是由颗粒分离向聚合演化。揭示菰属与稻属在稻族中均为原始类群,早在远古时代,可能起源于一共同祖先,以后平行向前发展,即一支为由多年生菰向一年生菰演化,另一支为由稻属向假稻属、山涧草属等演化。此两支在细胞与胚胎上明显不同,即菰属的染色体为 n = 15, 17, 胚为

Table 3 Species of Zizania L. and its relatives examined

Taxa	Voucher		
Zizania aquatica subsp. aquatica	S. L. Chen 87730, 87816 (cultivated in N. B. G. **, seeds from Maryland, U. S. A.)		
Z. aquatica var. subbrevis Boivin	Canada, Ontario: S. Brisson 67155 (Topotype)*****		
Z. aquatica subsp. brevis (Fass.) S. L. Chen	U. S. Nat. Herb. *** No. 2241530; Canada: Jason 8 Swallen 9703; W. G. Dore 47-961.		
Z. palustris subsp. palustris	S. L. Chen 8768 (cultivated in N. B. G**., seeds from Minnesota, U.S.A.)		
Z. palustris subsp. palustris f. purpurea Dore	Canada, Ottawa, W. G. Dore & R. J. Moore 10587 (Holotype)*****		
Z. palustris subsp. interior (Fass.) S. L. Chen	U. S. A., Minnesotia E. E. Terrell 4491,***		
Z. lasifolia (Griseb.) Turoz. ex Stapf	China: Jiangsu, S. Y. Hu & F. X. Liou without number, 7/9, 1984.**		
Z. mezii Prod.	cultivated in New Zealand; U. S. Nat. Herb. No. 1505038***.		
Z. texana Hitchc.	U. S. A., Texas: Trelean without number, 11/6, 1970,****		
Zizaniopsis miliacea (Michx.) Doel & Aschers	U. S. A., Louisiana: A. Chase without number, 10/6, 1921.****		
Oryza sasiva L.	China, Anhui: F. Courtois 21622.**		
Leersia hexandra Sw.	China, Sichuan. X. Y. He 6855.**		
L. sayanuka Ohwi	China, Anhui: F. Courtois 26788.**		
Chikusichloa aquazica Koidz.	China, Jiangsu: F. Courtois 10381.**		
Ch. musica Keng	China, Hainan: F. C. How 73980**		
Hygroryza ariszasu (Retz.) Nees	China: Z. H. Hu 7900520.**		
Pharus lazifolius L.	Peru: Vasquez & Jaramillo 560****		

^{**} Nanjing Botanical Garden Mem. Sun Yat-sen, Nanjing, China, 标本藏江苏植物所标本室。

F + PP; 稻亚族的染色体为 x = 12, 胚为 F + FP, 鲜有 F + PP。据此,近代不少禾本科分类学者主张将菰属独立成菰亚族 subtribe Zizaniinae。

再仔细观察花粉外壁的纹饰,菰与水稻更相似,同为1或3细颗粒形成团状,团间有 裂隙。它们在地理分布上也较近,如水稻几遍布全世界,而菰分布于东亚,波及夏威夷群岛。得克萨斯菰与拟菰的花粉外壁同为单个细小颗粒均匀分布,其与两种一年生菰均分

^{***} United state National Herbarium, Washington, D. C. U. S. A. 标本即藏该室。

^{****} 藏于 Herbarium of Missouri Botanical Garden, U. S. A.

^{*****} 藏于 Vascular Plant Herbarium of Biosystematics Research Centre, Canada,

表 4 菰属及其有关

Table 4 Comparison of pollen morphology

分类等级 Taxa	形 状 Shape	大 小 Size (µm)	
Zizania aquatica subsp. aquatica	近珠形至卵形 subspheroidal to oval	(35-41.5)40× (32.5-45)39.5	
Z. aquatica var, subbrevis	同 上 ditto		
Z. aquasica subsp.	近球形至卵形 ,粗糙 subspharoidal to oval, rugosus	(39.5 -50)40× (40-52.5)50	
Z. palustris subsp. palustris	近球形至卵形,粗糙且褶皱 subspheroidal to oval, rugose and plicate	(42.5—51.25)45× (26.25—30)28.75	
Z. palustris subsp. interior	近球形至卵形 subspheroidal to oval	$(22.5-26.25)25 \times (23.75-27.5)26.5$	
Z. lasifolia	. 近卵形至球形,多褶 near oval to subspheroidal, strongly plicate	(38.75-50)47.5× (30-37.5)32.5	
Z. mezii	同上 ditto	(47.5-56.25)52.5× (30-32.5)31.25	
Z. texans	近球形至卵形,多皱褶 subspheroidal to oval, strongly rugose and plicate	(48.75—51.25)50× (26.25—35)30	
Zizaniopsis milicea	近球形至卵形 subspheroidal to oval		
Oryza sativa	近球形至卵形,少褶 subspheroidal to oval, slightly plicate		
Leersia hexandra	近球形至卵形 subspheroidal to oval	(35-42.5)37.5× (18.75-25)20	
L. sayanuka	同。上 ditto	(47.5—52.5)51.25× (30—37.5)31.25	
Chikusichloa aquatica	近卵形至近球形 near oval to subspheroidal	(57.5—65)65.75× (40—53.75)42.5	
Ch. mutica	同 上 ditto	$(35-37.5)36.25 \times (31.25-36.25)33.75$	
Hygroryza aristata	近卵形至近球形,多皱褶 near oval to subspheroidal; stro- ngly rugose and plicate		
Pharus latifolius	近球形至卵形 subspheroidal to oval	(42.5-43.75)40× (22.5-30)25	

属种花粉形态比较衰

between Zizania and its relatives

萌 发 孔	外壁纹饰 Sculpture of Exine		01040
Aperture	光学显微镜下 under LM	扫描电镜下 under SEM	plate
孔周围略增厚,孔盖椭圆形,宿存 slightly thickened at the margin of pore; operculum elliptic, persistent	细小颗粒状 granules minute	1-2-(3)细小颗粒形成大小均匀的团 状纹饰 1-2-(3) minute granules aggregated in uniform size	1;1,7
同 ditto	同上 ditto	1-3细小颗粒形成大小均匀的团状纹饰 1-3 minute granules aggregated in uniform size	1:2.
			1:8.
内陷,孔周围明显加厚,孔盖脱离 concave, strongly thickened at the margin of pore; operculum deciduous	同上 ditto	1—3细小颗粒形成大小均匀的团状纹饰 1—3 minute granules aggregated in uniform size	1:3,9.
孔周围加厚,孔盖圆形,宿存 thickened at the margin of pore; operculum circular, persistent	同上 ditto	(1)—2—4细小颗粒形成大小均匀的团 状纹饰 (1)—2—4 minute granules aggregated in uniform size	1;4,10
孔周围很增厚,孔盖宿存 strongly thickened at the margin of pore; operculum persistent	同上 ditto	1 或 3 细小颗粒形成大小均匀的纹状纹饰 l or 3 minute granules aggregated in uniform size	1:5,12.
同 ditto	同上 ditto	同上 ditto	1:6
內陷,孔周围明显增厚,孔盖圆形,宿存 concave, strongly thickened at the margin of pore; operculum circular, persistent	同上 ditto	· 单个细小颗粒均匀密布 minute granules single, evenly and densely distributed	1:11,
孔周围不明显加厚,孔盖长圆形,宿存 obscurely thickened at the margin of pore; operculum oblong, persistent	同上 ditto	同上 ditto	2:2,7.
内陷;孔周围很加厚,孔盖圆形,宿存 concave, strongly thickened at the margin of pore; operculum circularis, persistent	同上 ditto	1 与 2—(4)细小颗粒组成大小均匀的纹饰 1 or 2—(4) minutes granules ag- gregated in uniform size	2:3.
孔周围不明显加厚,穿孔,孔盖长圆形,宿存 obscurely thickened at the margin of pore; distinctly perforate, opercu- lum oblong, persistent	同上 ditto	多个细小颗粒集成团块状,有穿孔 many minute granules aggregated in group; perforate between them	2:4,8.
孔周围加厚,孔盖脱落 thickened at the margin of pore; operculum deciduous	同上 ditto	1—4 细小颗粒组成片状纹饰,有裂隙 1—4 minute granules aggregated in small piece; rimos between them	2:9
	同上 ditto	多个细小颗粒组成大小不均匀的片沟, 其间有大小裂隙 many minute granules aggregated in large or small piece; small rimos between them.	2:11
内陷,孔周围加厚,孔盖宿存 concave, thicked at the margin of pore; operculum persistent	同上 ditto	许多细小颗粒组成鳞片状 many minute granules aggregated in scale-formed	2:5,12
孔周围明显加厚,孔盖宿存 strongly thickened at the margin of pore; operculum persistent	同上 ditto	多个细小颗粒组成大小不均匀的团状纹饰 many minute granules aggregated in large or small group	2:6,10
	同上 ditto		

布于北美 (Clayton 1986, Terrell 1978),其中拟菰可波及南美洲。再结合它们在花序形态与细胞形态上的明显区别,如菰的染色体为 n=17,圆锥花序的中部各分枝上混生有雄小穗及雌小穗;得克萨斯菰与两种一年生菰的染色体为 n=15,圆锥花序的上部分枝均为雌性,下部分枝均为雄性,在各分枝上无雌雄小穗混生的现象。据此,可推测它们有一共同的祖先(其胚为F+PP,染色体为 x=5),此祖先现已灭迹,由它起源而平行演化成现在的两支,即一支为分布于东亚的菰,另一支为分布于北美的三种菰,即得克萨斯菰、水生菰及沼生菰。

(四) 分类问题的处理: 表 2 显示出各分类学家对本属下所包含的种类各有不同的处理意见。本项研究,基本赞同 Terrell(1978)、Terrell 和 Robinson(1974),Terrell 和 Wergin (1979, 1981)等学者的观点,在菰属下分成 4 种。此外,在属内种间的处理上也都符合我们对其它特征所研究的结果,如从表 4 及图版 1 上可以看到 Z. latifolia 与 Z. mezii 的花粉形态很相似,应合并为一种;变种 Z. aquatica var. subbrevis Boivin 的花粉形态特征与水生菰基本相似,不赞同此变种成立。又如矮生菰的花粉外壁粗糙,不同于水生菰,结合它们叶片表皮微形态的硅质体也明显不同,应作亚种处理成 Z. aquatica subsp. brevis (Fass.) S. L. Chen (1989),同样,湖生菰花粉的孔盖宿存,明显区别于沼生菰的孔盖脱落,结合叶片表皮微形态与孕花外稃表皮微形态所具的硅质体也明显有别,应作亚种处理成 Z. palustris subsp. interion (Fass.) S. L. Chen (1989)。根据花粉形态的研究,在菰属内有下列 4 种 2 亚种。即菰 Zizania latifolia (Griseb.) Turcz。ex Stapf,得克萨斯菰 Z. texana Hitchc.,水生菰 Z. aquatica subsp. aquatica,矮生菰 Z. aquatica subsp. brevis (Fass.) S. L. Chen (1989)。

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图版说明 Explanation of plates

Plate 1 1-6, under SEM, 7-12, (×1500) under LM: 1.7. Zizania aquasica subsp. aquasica; 2. Z. aquasica var. subbrevis; 3, 9. Z. palustris subsp. palustris; 4. 10. Z. palustris subsp. interior; 5, 12. Z. latifolia; 6. Z. mesii; 8. Z. aquasica subsp. brevis; 11. Z. sexana.

Plate 2 1-6. under SEM, 7-12. (×1500) under LM: 1. Zizania texana; 2,7. Zizaniopsis miliacea; 3. Oryza sativa; 4, 8. Leersia hexandra; 5, 12. Chikusichloa mutica; 6, 10. Hygroryza aristata; 9. Leersia sayanuka; 11. Chikusichloa aquatica.

(上接第51页)

本刊力求办成一个培养和提高植物分类学研究队伍的"学校"。我们鼓励青年科学工作者投稿,对他们的稿件,我们除认真审查、提出详细修改建议外,有时,为了保证文章有较高的水平,我们还要进行反复推敲,请专家帮助修改。这样,自该刊创办以来作者队伍不断扩大,如1988年新作者有20人,占该年作者总数的47.6%。1989年,新作者占24人,占该年作者总数的55.8%。

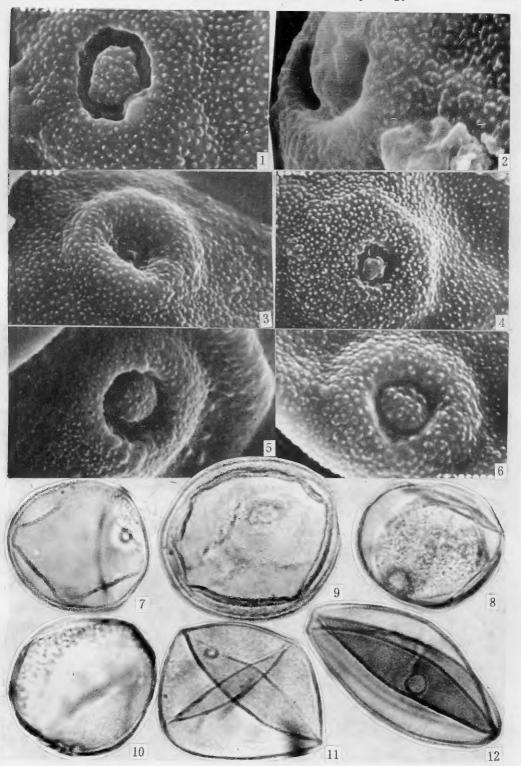
总之,40年来《植物分类学报》为本学科的发展,为出成果、出人材发挥了应有的作用。今后,将继续贯彻党的科技政策,贯彻"双百"方针,真实地反映我国植物分类学的进展和水平。我们决心尽量缩短刊出周期,进一步改进编排设计,使之更标准化、规范化;使附图更精确,文字更为简明扼要、数据更为准确、文献无误。我们将继续密切与读者、作者、审者的联系,共同把刊物办得更好。

《植物分类学报》40 年来的成就与历届编委和主编的认真、负责、严格把关及编辑部所有同志的辛勤劳动分不开,尤其应该感谢广大作者、审者和读者的关心、支持和热情帮助。我们没有忘记为本刊作过贡献的先辈们,更希望广大作者、读者和审者一如既往地关注我们的学报,继续给予热情支持,积极投稿,及时给我们批评和建议,使本刊办得更加出色。

植物分类学报编辑委员会 1991 年 2 月

Chen Shou-liang et al.: A Systematic and Evolutionary Study

of Zizania L. (Gramineae) - Pollen Morphology Plate 1



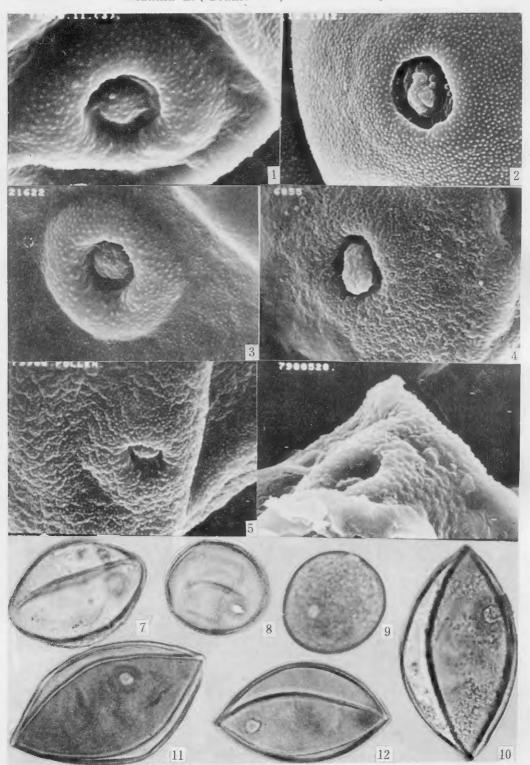
See explanations at the end of text

陈守良等: 菰属系统与演化研究一花粉形态

图版2

Chen Shou-liang et al.: A Systematic and Evolutionary Study of Zizania L. (Gramineae)—Pollen Morphology

Plate 2



See explanations at the end of text